Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*

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Abstract: The crustacean zooplankton communities in Lakes Michigan and Huron and the central and eastern basins of Lake Erie have shown substantial, persistent changes since the invasion of the predatory cladoceran *Bythotrephes* in the mid-1980s. A number of cladoceran species have declined dramatically since the invasion, including *Eubosmina coregoni*, *Holopedium gibberum*, *Daphnia retrocurva*, *Daphnia pulicaria*, and *Leptodora kindti*, and overall species richness has decreased as a result. Copepods have been relatively unaffected, with the notable exception of *Mesocyclops edax*, which has virtually disappeared from the lakes. These species shifts have for the most part been consistent and equally pronounced across all three lakes. Responses of crustacean species to the *Bythotrephes* invasion do not appear to be solely a consequence of size, and it is likely that other factors, e.g., morphology, vertical distribution, or escape responses, are important determinants of vulnerability to predation. Our results indicate that invertebrate predators in general, and invasive ones in particular, can have pronounced, lasting effects on zooplankton community structure.

Résumé : Les communautés de crustacés zooplanctoniques des lacs Michigan et Huron et des cuvettes centrale et orientale du lac Érié ont subi des changements importants et durables depuis l'invasion du cladocère prédateur *Bythotrephes* au milieu des années 1980. Plusieurs espèces de cladocères ont vu leur abondance décliner de façon spectaculaire depuis l'invasion, en particulier, *Eubosmina coregoni, Holopedium gibberum, Daphnia retrocurva, Daphnia pulicaria* et *Leptodora kindti*, ce qui a fait baisser la richesse globale en espèces. Les copépodes ont été peu affectés, avec l'exception notable de *Mesocyclops edax* qui est pratiquement disparu des lacs. Ces changements spécifiques se sont produits en général de façon semblable et avec la même intensité dans les trois lacs. Les réactions des espèces de crustacés à l'invasion de *Bythotrephes* ne semblent pas se faire seulement en fonction de la taille; il est donc probable que d'autres facteurs, tels que la morphologie, la répartition verticale et les comportements d'évitement, jouent un rôle important dans leur vulnérabilité à la prédation. Nos résultats indiquent que les invertébrés prédateurs en général, et les prédateurs envahisseurs en particulier, peuvent avoir un effet considérable et durable sur la structure de la communauté zooplanctonique.

[Traduit par la Rédaction]

Introduction

The ability of selective predation by vertebrates to substantially alter the size and composition of zooplankton communities has long been recognized (Hrbáček 1960; Hrbáček et al. 1961; Brooks and Dodson 1965); however, substantially less is known about the role of invertebrate predators in shaping zooplankton community structure. Numerous studies have documented the ability of invertebrate predation to mediate shifts in the size of zooplankton populations, particularly in the absence of strong vertebrate predation pressure (McQueen 1969; Dodson 1974; de Bernardi and Giussani 1975), but its importance in structuring zooplankton communities in the presence of vertebrate planktivores is generally considered to be low (Zaret 1980; de Bernardi et al. 1987; Hansson and Tranvik 1996).

The invasion of new predatory invertebrates into aquatic systems offers an opportunity to assess the effects of invertebrate predation on zooplankton community structure. Such an opportunity presented itself during the mid-1980s when *Bythotrephes longimanus* (initially referred to as *B. cederstroemi*), a large predatory cladoceran native to northern Europe and Asia, invaded the Laurentian Great Lakes. This species was first found in Lake Ontario in 1982 (Johannsson et al. 1991) and subsequently spread to all five Great Lakes (Bur et al. 1986; Evans 1988; Cullis and Johnson 1988), es-

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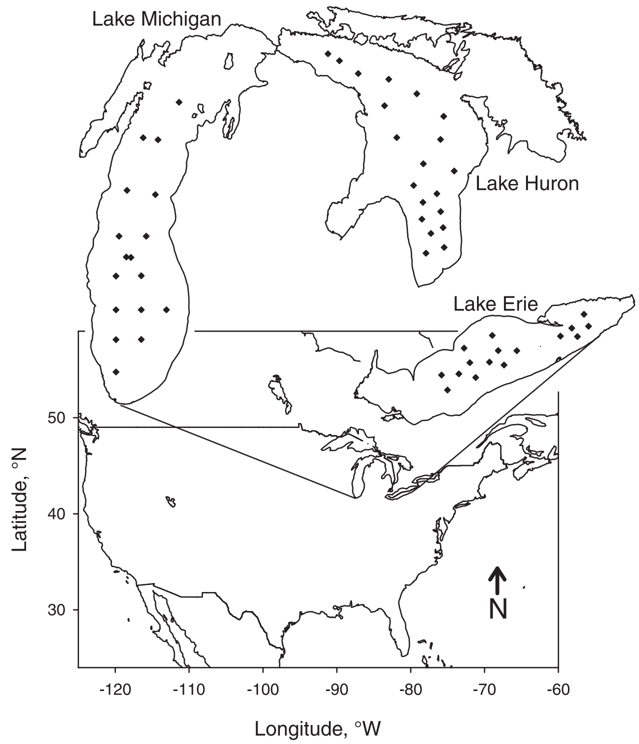
tablishing persistent populations in all but Lake Ontario and the western basin of Lake Erie. It has since spread to 50 inland Ontario lakes (Therriault et al. 2002), as well as several inland lakes in the United States (Yan and Pawson 1998). The effects of *B. longimanus* on the zooplankton community in Lake Michigan were particularly well documented during the initial years of the invasion (Lehman 1987, 1988). These studies indicated a pronounced shift in cladoceran community composition coincident with the appearance of *Bythotrephes* (Lehman 1988; Branstrator and Lehman 1991; Lehman and Cáceres 1993), as well as changes in the abundances of several rotifer species (Sandgren and Lehman 1990). To date, however, there have been no long-term assessments of the potential impacts of *Bythotrephes* on the Great Lakes. Elucidation of such impacts and their persistence requires long-term, internally consistent data sets. Although the importance of exploiting long-term data sets to elucidate impacts of freshwater invaders has been stressed (Yan et al. 2001), to date only one such data set has come to light: that of Harp Lake, Ontario (Yan and Pawson 1997; Yan et al. 2001, 2002). The Great Lakes National Program Office (GLNPO) of the US Environmental Protection Agency has been monitoring the Laurentian Great Lakes since 1983. Thus, a detailed, internally consistent and spatially extensive data set exists of zooplankton community composition during both the pre- and post-invasion periods. Here we make use of this unique data set to examine the impacts that *B. longimanus* has had on the crustacean zooplankton communities of Lakes Huron, Michigan, and Erie (monitoring of Lake Superior did not begin until after the appearance of *Bythotrephes* in that lake). Specifically, we were interested in determining whether changes have occurred in zooplankton community structure since the invasion of *B. longimanus*, how persistent any such changes have been, and how consistent these have been across the three lakes.

Methods

Lakes Erie, Michigan, and Huron were sampled annually during late summer (1 August – 4 September), a period that likely coincided with peak cladoceran abundances in Lakes Michigan and Huron (Wells 1960; Watson and Carpenter 1974), but not in Lake Erie where maximum populations occur in late June and July (Johannsson et al. 1999). Sampling was conducted between 1983 and 1999 with the following exceptions: Lakes Huron and Erie were not sampled in 1992, 1994, and 1995, and data from 1997 are not available for any of the three lakes. Because *Bythotrephes* has failed to establish substantial populations in the western basin of Lake Erie, results from that lake will be restricted to the central and eastern basins. The two basins of Lake Erie are morphometrically distinct; most of the central basin is 20 to 24 m deep, whereas depths in the smaller eastern basin exceed 60 m. Therefore they are treated separately in all analyses. Sampling was spatially extensive throughout the offshore waters of all lakes (Fig. 1). Zooplankton samples were collected with vertical net tows taken at each station from either 20 m deep or 1 m above the bottom, whichever was shallower, with a 0.5-m-diameter, 64-μm-mesh conical net (diameter:length = 1:3). The net was equipped with a flow meter and appropriate corrections were made for filter-

Fig. 1. Map of sampling stations in Lakes Michigan, Huron, and Erie. Not all stations were sampled in all years.



ing efficiency. Since 1997, additional zooplankton tows have been taken from a depth of 100 m or 2 m from the bottom, whichever is shallower, using a 153-μm-mesh conical net. Data from these tows were used for comparisons of crustacean lengths but were not used in the assessment of changes in historical densities.

Shipboard operations are conducted on a 24-h basis, and it is recognized that species undergoing diurnal vertical migration (DVM) could have been underestimated at stations sampled during the daytime. Because sampling times for zooplankton tows were not recorded for cruises before 1997, no corrections could be made for differences in time of day of collection. However, sampling runs on each lake typically take more than 24 h, and this should result in a mix of daytime and nighttime samples being taken for each lake in each year. Therefore, the main impact of using 20-m tows should be to increase intra-annual variability in density estimates, rather than to introduce any systematic interannual bias. We therefore feel that these data are representative of temporal trends in community composition and species densities. Populations of the deep-living species *Mysis relicta*, *Limnocalanus macrurus*, and *Leptodiaptomus sicilis*, however, cannot be accurately assessed with data from 20-m tows and will not be considered here.

After collection, samples were immediately narcotized with soda water and preserved with sucrose formalin solution (Haney and Hall 1973) approximately 20 min later. Samples were split in the laboratory using a Folsom plankton splitter, and four stratified aliquots were examined per sample using a stereoscopic microscope such that rare species were enumerated from the less dilute aliquots. On average, about 600 individuals were identified per sample. Crustacean taxonomy generally followed Balcer et al. (1984); other sources

Table 1. Lake-wide late summer densities (number·m^{-3}) of common crustacean zooplankton species in Lakes Michigan (MI), Huron (HU), and Erie (ER C, central basin; ER E, eastern basin) averaged over all years of study (1983–1999).

	Lake			
Species	MI	HU	ER C	ER E
Bythotrephes longimanus	11	10	32	23
Leptodora kindti	18	10	30	41
Diaphanosoma birgei	9	1	774	388
Holopedium gibberum	19	129	28	70
Daphnia mendotae	3 418	1 413	4 091	3 203
Daphnia longiremis	6	15	97	126
Daphnia pulicaria	164	74	171	154
Daphnia retrocurva	93	75	687	1 162
Eubosmina coregoni	28	118	663	618
Bosmina longirostris	1 762	945	2 748	1 597
Total cladocerans	5 531	2 936	9 345	7 408
Leptodiaptomus ashlandi	1 917	507	197	44
Leptodiaptomus minutus	1 009	1 151	335	306
Leptodiaptomus siciloides	0	0	57	179
Skistodiaptomus oregonensis	101	110	3 326	2 280
Diaptomid copepodites	6 657	11 832	8 176	10 050
Epischura lacustris	71	57	187	246
Epischura copepodites	154	562	1 146	1 894
Total calanoids	10 038	14 336	13 464	15 011
Acanthocyclops vernalis	1	5	67	130
Diacyclops thomasi	1 525	814	911	399
Cyclopoid copepodites[a]	4 106	4 572	4 222	3 942
Mesocyclops edax	23	38	1 196	762
Mesocyclops copepodites	16	110	1 510	619
T. extensus copepodites	313	41	393	1 209
Total cyclopoids	6 367	5 659	8 587	7 990

Note: Group totals include all species, including those not shown.
[a]Mostly *Diacyclops thomasi*.

consulted included Brooks (1959), Evans (1985), and Hudson et al. (1998). Immature calanoids and cyclopoids were identified to the lowest taxonomic level possible, usually suborder or genus. Length measurements were made on the first 20 individuals of each species encountered per sample. *Bythotrephes* was measured from the anterior margin of the eye to the insertion point of the first pair of spines on the caudal process; corrections were not made for shrinkage in formalin. Differences in *Bythotrephes* lengths among the four lake areas were assessed using a generalized linear model (GLM) with stations (n = 8–26) as a random factor nested within lake areas and individual length measurements from each station constituting within-station replicates. Between 120 and 384 individual length measurements were used per lake area. Specific differences between pairs of lake areas were assessed using Tukey–Kramer pairwise comparisons. Only measurements from 100-m tows taken in 1999 were used for this analysis.

Changes in densities of major groups and individual species before and after the *Bythotrephes* invasion were assessed using either a t test or, where assumptions of normality and homoscedasticity were not met, the Mann–Whitney rank sum test. Because trends were assessed using annual lake-wide averages, we defined the initial year of invasion as the first year in which *Bythotrephes* appeared at a majority of sites in each lake. Thus, post-invasion years began in 1986 for Lakes Huron and Erie and in 1987 for Lake Michigan. While referred to for brevity as pre- and post-invasion periods, these more properly correspond to pre- and post-lake-wide colonization periods. The conservative approach of using annual lake-wide average values rather than individual station values was adopted, as in the latter case, extremely high sample sizes would have permitted the detection of minor differences unlikely to be of ecological importance. Temporal autocorrelation was tested for using a lag of one time period; no significant effects were found for any species–lake combination. Significance was assessed at $\alpha = 0.05$. Although we recognize that a large number of tests using similar null hypotheses were conducted in our analyses, we were not testing a universal null hypothesis, i.e., a significant effect in any of the comparisons would not have implied a significant effect overall, nor would it have lessened interest in the results of subsequent tests. Therefore, no Bonferroni-type corrections were deemed necessary, and significance was assessed in all cases at $\alpha = 0.05$. The reader is advised to interpret the results accordingly.

Patterns in zooplankton community composition across the lakes were explored with the use of detrended correspondence analysis (DCA), using the program CANOCO version 4.0. This is an ordination technique that extracts axis scores

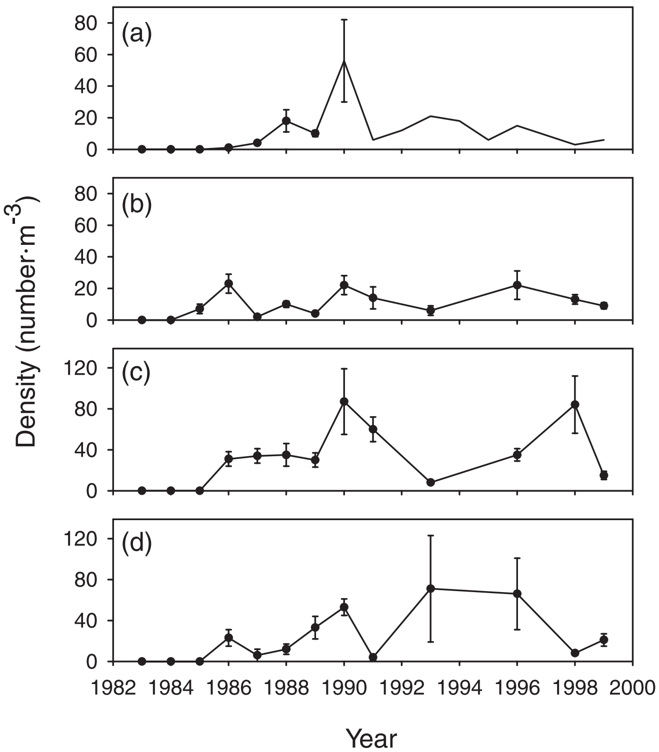


Fig. 2. Average lake-wide (basin-wide in the case of Lake Erie) late summer densities of *Bythotrephes* in (*a*) Lake Michigan, (*b*) Lake Huron, and (*c*) central and (*d*) eastern basins of Lake Erie. Note differences in scale between graphs. Bars represent one standard error.

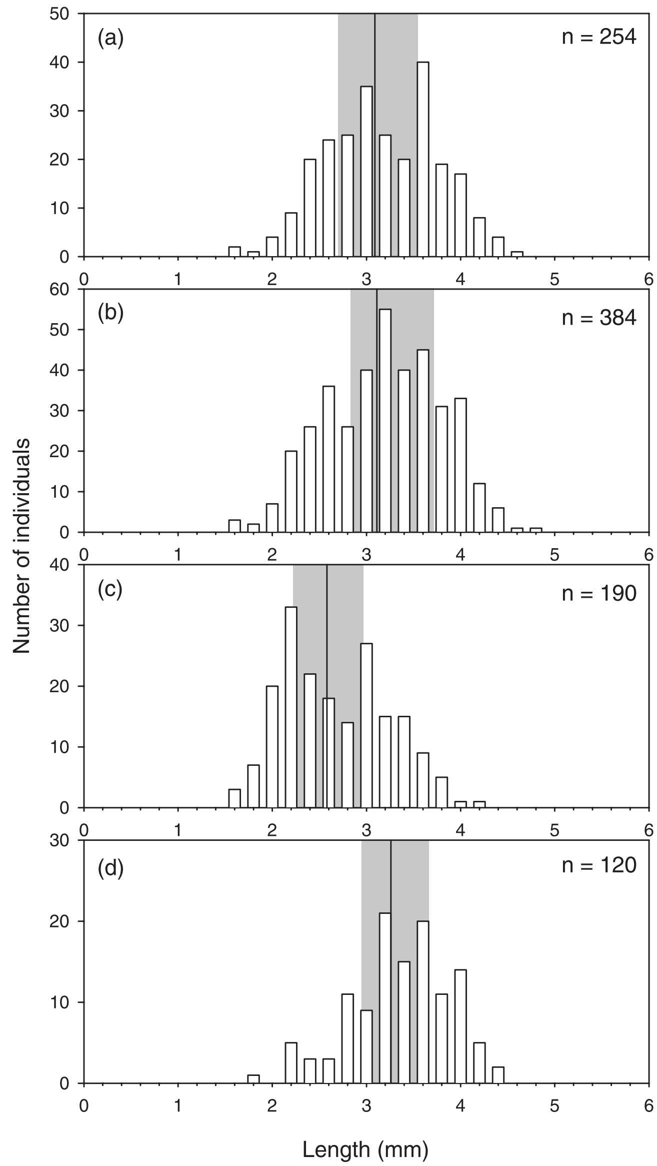


Fig. 3. Size–frequency distributions of *Bythotrephes* lengths in (*a*) Lake Michigan, (*b*) Lake Huron, and (*c*) central and (*d*) eastern basins of Lake Erie in 1999. Vertical reference lines indicate mean lengths; shaded areas indicate interquartile ranges.

from samples on the basis of species composition such that samples with similar species composition are close by, and those with dissimilar species composition are far apart. Only those species constituting more than 1% of total abundances in any sample were included in the analysis. Densities were converted to natural logarithms before analysis to reduce the undue influence of dominant species.

Results

When averaged over all years of the study (1983–1999), diaptomid copepodites were numerically dominant in all lakes during late summer (Table 1). Adult calanoids were represented mostly by *Leptodiaptomus minutus* and *Leptodiaptomus ashlandi* in Lakes Michigan and Huron, whereas *Skistodiaptomus oregonensis* and *Epischura lacustris* were most prevalent in Lake Erie. Cyclopoids were represented almost exclusively by *Diacyclops thomasi* in Lakes Huron and Michigan, with *Mesocyclops edax* co-dominant in Lake Erie. *Daphnia mendotae* was the dominant cladoceran across all lakes, although several other daphnids, including *Daphnia retrocurva*, *Daphnia pulicaria*, and *Daphnia longiremis*, were also found, along with the smaller cladocerans *Bosmina longirostris* and *Eubosmina coregoni*.

Bythotrephes longimanus was first found in North America in Lake Ontario in 1982 (Johannsson et al. 1991), although substantial populations have never become established in the lake. *Bythotrephes* was subsequently found at two stations in southern Lake Huron during a GLNPO cruise in December 1984 (Bur et al. 1986). In August 1985, populations of this organism were still fairly small and largely restricted to the southern portion of the lake. By 1986 it was seen in sizeable numbers at most stations. *Bythotrephes* was first found in Lake Erie during a GLNPO cruise in mid-November 1985. At that time, individuals were found in vertical net tows in the western and central basins and in the western-most portion of the eastern basin. By August of 1986, populations were firmly established in the central and eastern basins, where this organism has been seen consistently during GLNPO's annual August cruises. In contrast, *Bythotrephes* has been virtually absent from the western basin. *Bythotrephes* was first found in Lake Michigan at two offshore sites in the central and northern area of the lake during a GLNPO cruise on 21–22 August 1986. By August 1987, the organism was distributed throughout the lake and has since maintained a

Fig. 4. Average late summer species richness (including *Bythotrephes*) per sample observed in (*a*) Lake Michigan, (*b*) Lake Huron, and (*c*) central and (*d*) eastern basins of Lake Erie. Bars represent one standard error; arrows indicate first post-invasion year; broken reference lines indicate average pre-invasion species richness.

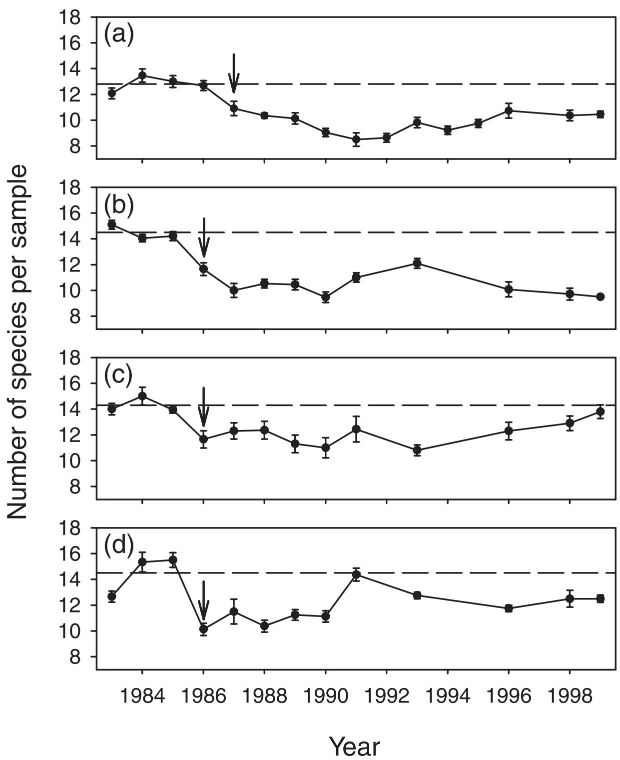
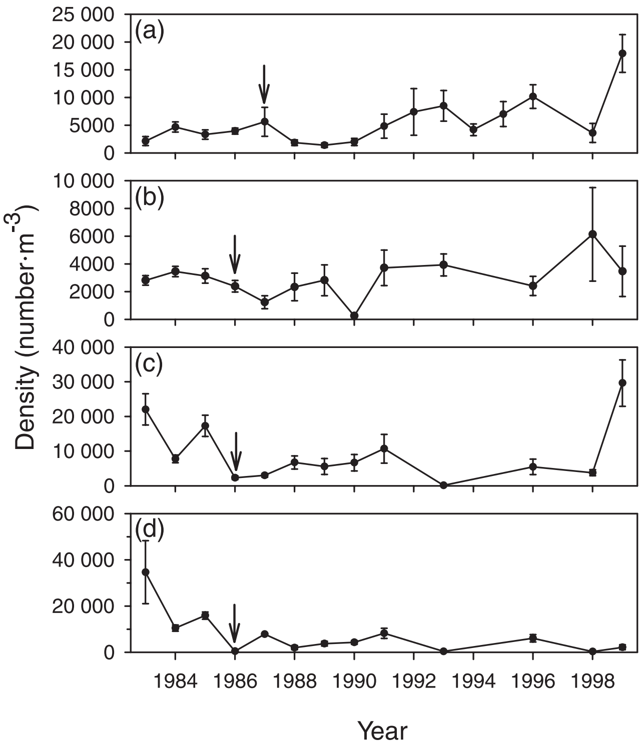


Fig. 5. Average lake-wide (basin-wide in the case of Lake Erie) late summer densities of cladocerans (excluding *Bythotrephes*) in (*a*) Lake Michigan, (*b*) Lake Huron, and (*c*) central and (*d*) eastern basins of Lake Erie. Note differences in scale between graphs. Bars represent one standard error; arrows indicate first post-invasion year.



persistent, if somewhat variable, presence in the offshore waters.

Population densities of *Bythotrephes* have been highest in the central basin of Lake Erie, where the overall late summer average since the establishment of the population in 1986 has been 41 m^{-3} (Fig. 2). Densities have been nearly as high in the eastern basin (mean = 32 m^{-3}), although somewhat more variable. Densities in Lakes Huron and Michigan have been much lower (13 and 10 m^{-3}, respectively) and have only occasionally approached the levels seen in Lake Erie. Although populations have shown some fluctuations over the years, the species is firmly established in all three lakes.

Bythotrephes lengths in 1999 were highest in the eastern basin of Lake Erie (mean = 3.26 mm), intermediate for Lakes Michigan and Huron (mean = 3.09 and 3.11 mm, respectively), and lowest in the central basin of Lake Erie (mean = 2.58; Fig. 3). The GLM procedure indicated that statistical differences in lengths existed between the different lake areas (F = 9.198, p = 0.0001). Pair-wise comparisons showed statistically significant differences in mean lengths between all lakes except Lakes Michigan and Huron.

Crustacean species richness in August fell in all lakes immediately following the *Bythotrephes* invasion (Fig. 4). Pre-invasion species richness averaged approximately 14 species·$sample^{-1}$, except in Lake Michigan where richness was slightly lower (12.8). Since the invasion, average richness has fallen between 16% (Erie, central basin) and 28% (Michigan), with all decreases determined to be statistically significant by the Mann–Whitney rank sum test (P < 0.001). Richness values during the 1990s were slightly higher than those recorded immediately after the invasion in the eastern basin of Lake Erie and, to a lesser extent, in Lake Michigan. However, lake-wide late summer averages after the invasion have remained below the pre-invasion average for all years of the study in all lakes.

Dramatic effects on abundances of major groups by and large were not seen. Total cladoceran abundances did decline notably in Lake Erie in the first year of invasion and remained relatively suppressed in both basins (Fig. 5). The difference between pre- and post-invasion abundances was statistically significant for the eastern basin (Table 2), but not the central basin, owing to unusually high cladoceran abundances in 1999. Excluding this year, the difference between the two periods was highly significant (t = 3.802, P = 0.003). A slight decrease in cladoceran abundance was seen in the years immediately following the invasion in Lake Michigan, although in neither Lake Michigan nor Lake Huron were statistically significant differences between the two periods seen. No clear patterns were evident in calanoid abundance, and no statistically significant differences were found between the pre- and post-invasion periods. Similarly, no clear patterns were apparent in cyclopoid abundances, and no statistically significant differences were found between the pre- and post-invasion periods.

A number of crustacean species exhibited distinct changes in density coincident with the appearance of *Bythotrephes*. In many cases these changes were quite abrupt and consis-

Table 2. Results of *t* test (*t*), or Mann–Whitney rank sum test (*T*) where assumptions of normality and homoscedasticity are not met, of differences in late summer densities of crustacean species during the pre- and post-invasion periods in Lakes Michigan and Huron and the central and eastern basins of Lake Erie.

	Lake			
Species	Michigan	Huron	Central Erie	Eastern Erie
Leptodora kindti	T = 58	t = 5.372	t = 2.228	T = 25
	P = **0.004**	P = **<0.001**	P = **0.048**	P = 0.554
Daphnia pulicaria	T = 58	T = 36	T = 30	T = 30.5
	P = **0.004**	P = **0.014**	P = 0.146	P = 0.122
Daphnia retrocurva	T = 58	T = 30	t = 3.564	T = 35
	P = **0.004**	P = 0.15	P = **0.004**	P = **0.022**
Daphnia mendotae	t = –1.216	T = 25	t = 2.822	T = 36
	P = 0.244	P = 0.554	P = **0.017**	P = **0.014**
Daphnia longiremis			T = 8	t = –1.048
			P = **0.035**	P = 0.317
Diaphanosoma birgei			t = 2.592	T = 34
			P = **0.025**	P = **0.034**
Eubosmina coregoni	T = 58	T = 35	T = 35	T = 36
	P = **0.004**	P = **0.022**	P = **0.022**	P = **0.014**
Bosmina longirostris	T = 18	t = –1.205	T = 14	T = 21
	P = 0.06	P = 0.253	P = 0.272	P = 0.933
Holopedium gibberum	T = 50	t = 3.351	T = 34	T = 34
	P = 0.06	P = **0.006**	P = **0.034**	P = **0.034**
Total cladocerans	t = –1.130	t = 0.274	t = 1.549	T = 36
	P = 0.277	P = 0.789	P = 0.150	P = **0.014**
Mesocyclops edax	T = 53	T = 36	t = 3.476	T = 36
	P = **0.025**	P = **0.014**	P = **0.005**	P = **0.014**

Note: In all cases, a two-tailed null hypothesis was used. Probabilities significant at $\alpha = 0.05$ are shown in bold.

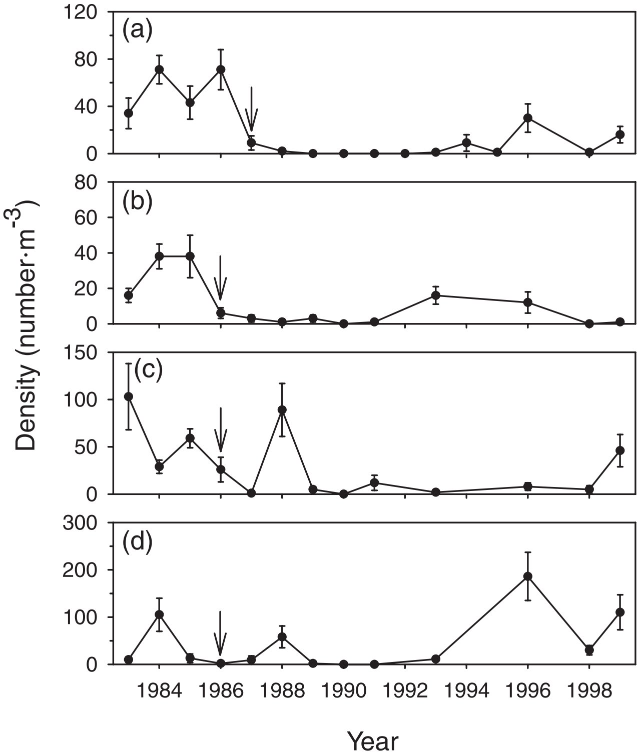
tent across all three lakes. Densities of the native predatory cladoceran *Leptodora kindti* declined markedly in both Lakes Michigan and Huron immediately after the invasion of *Bythotrephes* (Fig. 6). In both lakes, *Leptodora* was virtually absent from the open waters through the early 1990s, and although occasionally found in somewhat greater numbers since then, densities have consistently remained below pre-invasion levels. The situation was similar in the central basin of Lake Erie, although a particularly large *Leptodora* population was seen in 1988. In all three cases, post-invasion declines were statistically significant (Table 2). *Leptodora* populations have been more variable in the eastern basin of Lake Erie, and there has not been a clear reduction in densities since the appearance of *Bythotrephes*.

The large daphnid *D. pulicaria* was a sizeable component of the immediate pre-invasion communities of Lakes Michigan and Huron and has virtually disappeared from each lake since the invasion (Fig. 7). This species was only seen in sizeable numbers in 1984 in Lake Erie, so its subsequent absence from that lake is harder to ascribe to *Bythotrephes*. The smaller *D. retrocurva* declined immediately after the arrival of *Bythotrephes* in all three lakes (Fig. 7). This species seemed to recover in Lake Huron in the mid-1990s, exhibiting large but highly variable populations in 1991 and 1993. As with *D. pulicaria*, pre-invasion numbers were quite variable in Lake Erie, although population decreases were significant in all lakes but Huron (Table 2). In contrast to these daphnids, the dominant cladoceran in the lakes, *D. mendotae*, did not show a clear response to the appearance of *Bythotrephes* (Fig. 8). Populations have changed during the period of record, in particular, declining in Lake Erie and increasing in Lake Michigan during the 1990s. There is some suggestion of decreased densities during the initial year of invasion in Lake Erie, and overall *D. mendotae* populations have been statistically significantly lower in that lake in post-invasion compared with pre-invasion years. However, the major declines appear to have taken place 5 or more years after the invasion, suggesting causes other than *Bythotrephes*.

Two cladocerans that were found in significant numbers only in Lake Erie exhibited opposite responses to *Bythotrephes*. Post-invasion populations of *Diaphanosoma birgei* were statistically significantly lower in both basins of Lake Erie (Fig. 9), whereas *D. longiremis* appeared to increase during the post-invasion period, although this increase was only statistically significant in the central basin.

Among the smaller cladocerans, *E. coregoni* had been a relatively minor component of the crustacean communities in Lakes Michigan and Huron but was more prominent in Lake Erie. In all three lakes, this species declined precipitously immediately following the appearance of *Bythotrephes* (Fig. 10) and has since remained at very low levels. These changes were statistically significant in all lakes (Table 2). Populations of the closely related *B. longirostris* have generally increased during the post-invasion period (Fig. 10), although the timing of these increases has varied widely in the three lakes and, with the exception of the eastern basin

Fig. 6. Average lake-wide (basin-wide in the case of Lake Erie) late summer densities of *Leptodora kindti* in (*a*) Lake Michigan, (*b*) Lake Huron, and (*c*) central and (*d*) eastern basins of Lake Erie. Note differences in scale between graphs. Bars represent one standard error; arrows indicate first post-invasion year.



of Lake Erie, appear for the most part to have occurred substantially after the arrival of *Bythotrephes*. Another relatively minor component of the crustacean community, *Holopedium gibberum*, experienced dramatic and relatively sustained declines immediately following the arrival of *Bythotrephes* in all three lakes (Fig. 11), although its suppression has not been as complete as that of *E. coregoni*. The large population of *H. gibberum* seen in Lake Michigan in 1996 was due to an anomalously high count at a single station in that year. With the exception of this lake, the declines in *H. gibberum* have been statistically significant (Table 2).

By and large consistent, sustained changes in calanoid populations were not seen in any of the lakes coincident with the arrival of *Bythotrephes*. However, the cyclopoid copepod *M. edax* exhibited a very clear, statistically significant decline in all three lakes following the invasion, and populations have since remained extremely low (Fig. 11).

DCA ordination of crustacean communities indicated marked differences between pre- and post-invasion crustacean communities in all three lakes (Fig. 12). Although crustacean communities in Lakes Huron and Michigan were clearly differentiated from those in Lake Erie in the ordination, the trajectory of change between pre- and post-invasion communities was similar in all lakes: post-invasion samples exhibited an increase in axis 1 scores and a decrease in axis 2 scores relative to pre-invasion samples. The location of species in ordination space provides an indication of the relative importance of different taxa in differentiating between pre- and post-invasion communities; those with lower axis 1 scores and higher axis 2 scores should be most prominent in pre-invasion communities (Fig. 12). Most notable among such species were *D. retrocurva*, *D. pulicaria*, *H. gibberum*, *E. coregoni*, and *L. kindti*, which agrees with the observations made above. In addition, *D. birgei* and *M. edax* exhibited particularly low axis 1 scores, indicating their greater dominance in pre-invasion communities, although their position on axis 2 indicates that these taxa were more important in Lake Erie than in the other lakes.

Median lengths of cladoceran species from 1994 to 1999 (excluding the eastern basin of Lake Erie) showing post-*Bythotrephes* declines ranged from 0.5 to 1.08 mm and exhibited substantial overlap with those species whose populations were apparently unaffected by the invasion (Fig. 13). *Eubosmina coregoni* was the smallest of the impacted species, with a lower interquartile length of 0.4 mm and a median length of 0.5 mm. Three species with very similar size distributions, *H. gibberum* (interquartile range, 0.58–0.95 mm; median, 0.7 mm), *D. birgei* (interquartile range, 0.58–0.85 mm; median, 0.74 mm), and *D. longiremis* (interquartile range, 0.6–0.95 mm; median, 0.75 mm) showed differing responses to *Bythotrephes*, the first two declining and the latter species generally increasing. The two largest daphnids in the lakes, *D. mendotae* and *D. pulicaria*, also showed opposite responses, the former unaffected and the latter virtually eliminated. Lengths of these two species overlapped considerably, although *D. pulicaria* was extremely rare, so it is unclear how representative the few data available for it are.

Discussion

The crustacean communities in Lakes Michigan and Huron and the central and eastern basins of Lake Erie exhibited dramatic reductions in the populations of a number of mostly cladoceran species and a decline in species richness following the appearance of *Bythotrephes*. Direct predation by *Bythotrephes* offers the most parsimonious explanation for the restructuring of the cladoceran communities in Lakes Michigan, Huron, and Erie. Cladocerans are known to be a favored prey of this genus (Mordukhai-Boltovskaya 1958; Vanderploeg et al. 1993; Schulz and Yurista 1999), and nearly all of the species that exhibited declines in our study have been shown to be vulnerable to *Bythotrephes* predation through either field or laboratory studies. Our results also show strong agreement with those from Harp Lake, a Precambrian Shield lake in south-central Ontario invaded by *Bythotrephes* in the early 1990s that has been the subject of the most extensive studies of *Bythotrephes* effects in North America to date (Yan and Pawson 1997; Yan et al. 2001, 2002).

The lakes examined here have been subject to various forcings over the course of this study. However, the timing and abruptness of the changes seen in this study, and their consistency across the three lakes, argue strongly for *Bythotrephes* as the main causative factor in the restructuring of the crustacean communities. Nutrient levels in both Lakes Michigan and Erie have declined during the period under

Fig. 7. Average lake-wide (basin-wide in the case of Lake Erie) late summer densities of *Daphnia pulicaria* and *Daphnia retrocurva* in Lake Michigan, Lake Huron, and the central (Erie C) and eastern (Erie E) basins of Lake Erie. Note differences in scale between graphs. Bars represent one standard error; arrows indicate first post-invasion year.

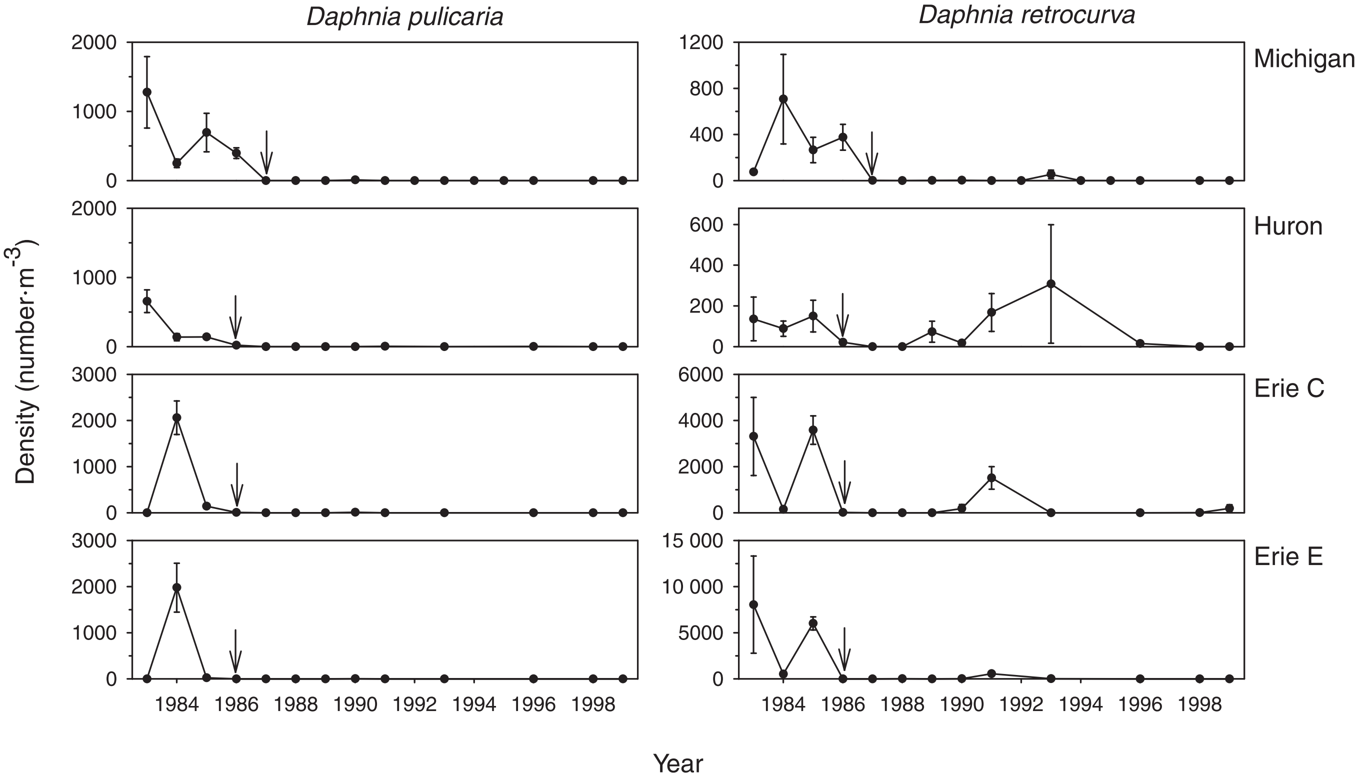
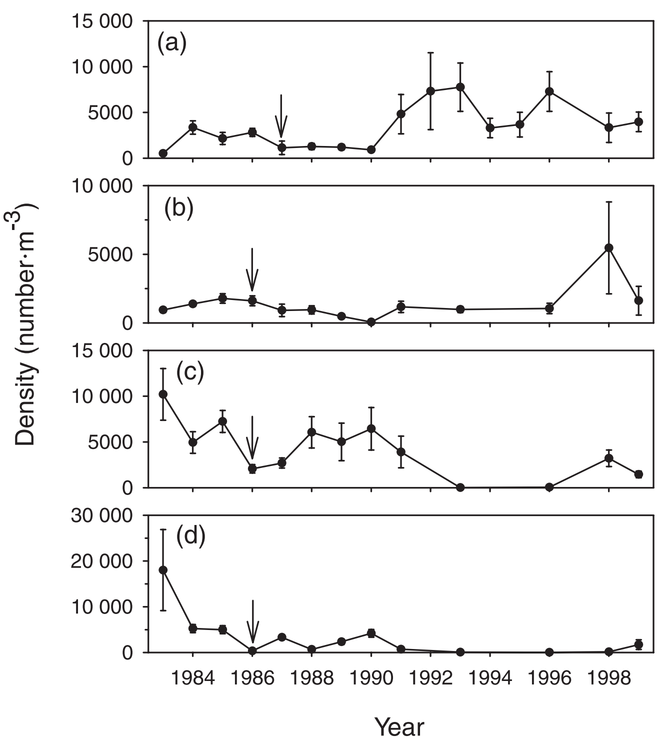


Fig. 8. Average lake-wide (basin-wide in the case of Lake Erie) late summer densities of *Daphnia mendotae* in (*a*) Lake Michigan, (*b*) Lake Huron, and (*c*) central and (*d*) eastern basins of Lake Erie. Note differences in scale between graphs. Bars represent one standard error; arrows indicate first post-invasion year.



consideration here (Charlton et al. 1999; Barbiero et al. 2002), but these changes have been gradual and are unlikely to have produced the sudden shifts in crustacean community composition seen. Also, the lack of nutrient reductions in Lake Huron would argue against this as a causative mechanism. All three lakes have been invaded by the zebra mussel, *Dreissena polymorpha* (Griffiths et al. 1991), an organism thought to have had pronounced impacts on community structure and trophic relations in parts of the Great Lakes (Leach 1993; Fahnenstiel et al. 1995; Holland et al. 1995). However, the chronology of the *Dreissena* invasion is not consistent with the timing of changes seen in this study. Colonization of the central basin of Lake Erie did not occur until 1988, with the eastern basin colonized the following year (Griffiths et al. 1991). Isolated nearshore populations only became established in Lakes Michigan and Huron in 1990. Most of the major shifts in crustacean populations in our study occurred before these colonization dates. It is harder to assess what role variations in fish stocks might have had on the shifts in crustacean communities seen in our study, although the notable declines in both large and small cladoceran species is inconsistent with the selective reduction in larger individuals that typically results from intense vertebrate planktivory (Brooks and Dodson 1965; Mills et al. 1987).

Our results indicate that the dramatic alterations in the daphnid community observed during the early post-invasion period in Lake Michigan (Lehman 1988, 1991) have persisted and that these changes have not been confined to Lake Michigan, but have occurred in Lake Huron and in the eastern and central basins of Lake Erie as well. These include

Fig. 9. Average basin-wide late summer densities of *Diaphanosoma birgei* and *Daphnia longiremis* in the central (Erie C) and eastern (Erie E) basins of Lake Erie. Bars represent one standard error; arrows indicate first post-invasion year.

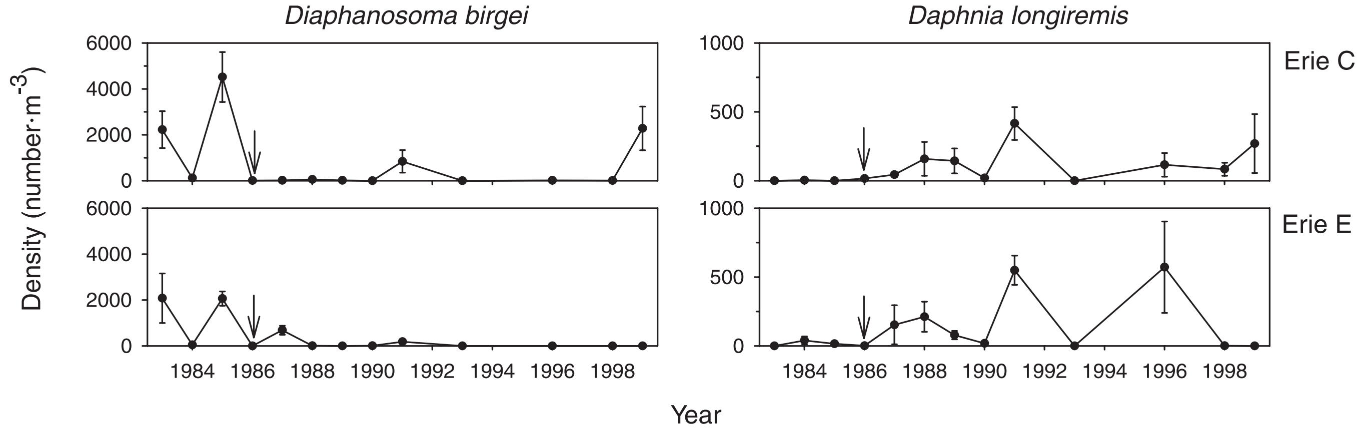
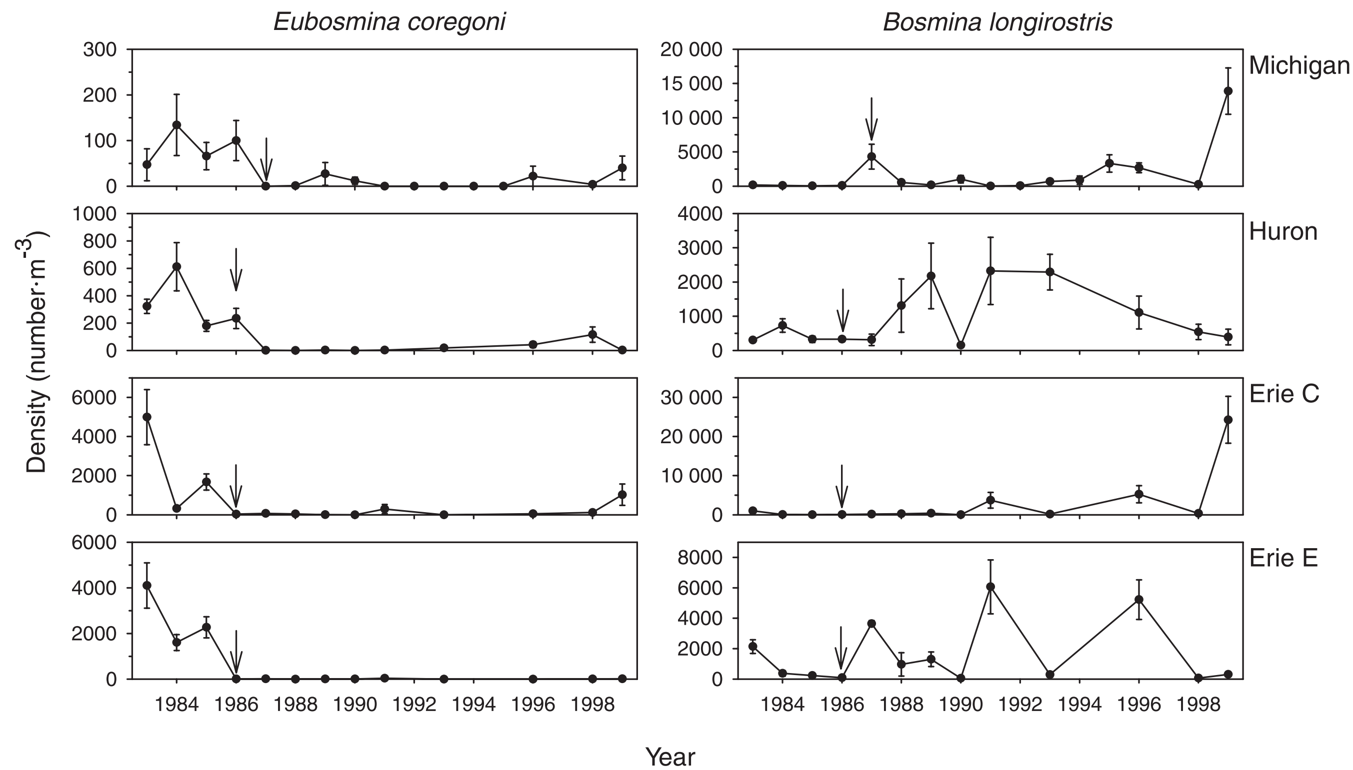
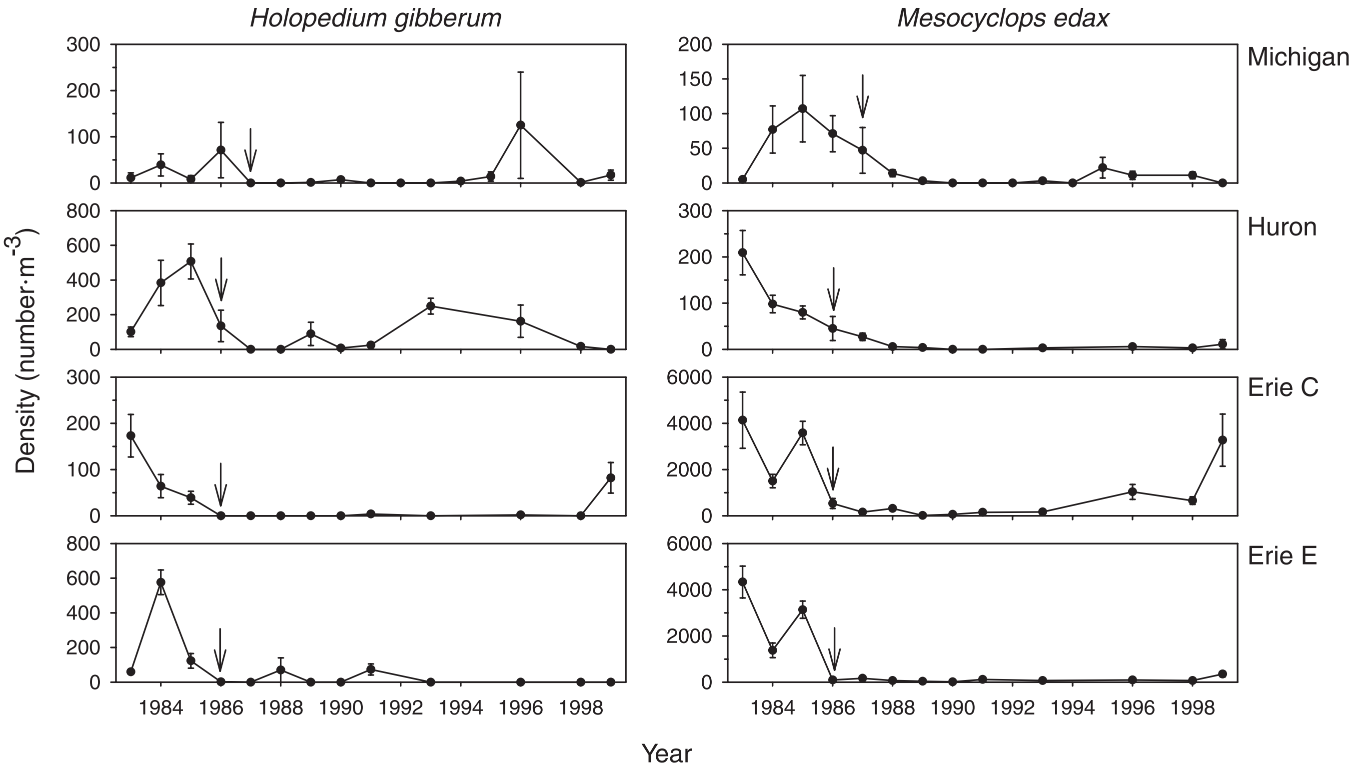


Fig. 10. Average lake-wide (basin-wide in the case of Lake Erie) late summer densities of *Eubosmina coregoni* and *Bosmina longirostris* in Lake Michigan, Lake Huron, and the central (Erie C) and eastern (Erie E) basins of Lake Erie. Note differences in scale between graphs. Bars represent one standard error; arrows indicate first post-invasion year.



the disappearance of *D. retrocurva* and *D. pulicaria* from the offshore waters and the subsequent sole dominance of the daphnid community by *D. mendotae* (Lehman 1991). The suppression of *D. pulicaria* has been the most complete of any species in our study, and *Bythotrephes* has been shown to prey upon *D. pulicaria* in the laboratory (Burkhardt and Lehman 1994; Schulz and Yurista 1999). However, the short history of *D. pulicaria* in Lake Michigan (Evans and Jude 1986) and the lack of substantial pre-invasion populations in Lake Erie (Davis 1968; Watson and Carpenter 1974) raises the possibility that other factors might have contributed to its absence from these lakes. *Daphnia retrocurva* has historically been co-dominant with *D. mendotae* in the offshore waters of Lake Michigan (Wells 1960; Evans and Jude 1986) and was also reported as a co-dominant daphnid with *D. mendotae* in Lake Erie in early studies (Chandler 1940; Bradshaw 1964; Watson and Carpenter 1974). Its post-invasion disappearance from both of these lakes has been pronounced. Although quantitative data are sparse, it does not appear to have been an important component of the crustacean community of Lake Huron (Watson and Carpenter 1974; Evans 1986). Yan and Pawson (1997) have also reported dramatic decreases in *D. retrocurva* abundance in Harp Lake following the *Bythotrephes* invasion, with no declines seen in *D. mendotae* abundance. Feeding experiments have shown the ability of

Fig. 11. Average lake-wide (basin-wide in the case of Lake Erie) late summer densities of *Holopedium gibberum* and *Mesocyclops edax* in Lake Michigan, Lake Huron, and the central (Erie C) and eastern (Erie E) basins of Lake Erie. Note differences in scale between graphs. Bars represent one standard error; arrows indicate first post-invasion year.



Bythotrephes to prey on *D. retrocurva* (Vanderploeg et al. 1993).

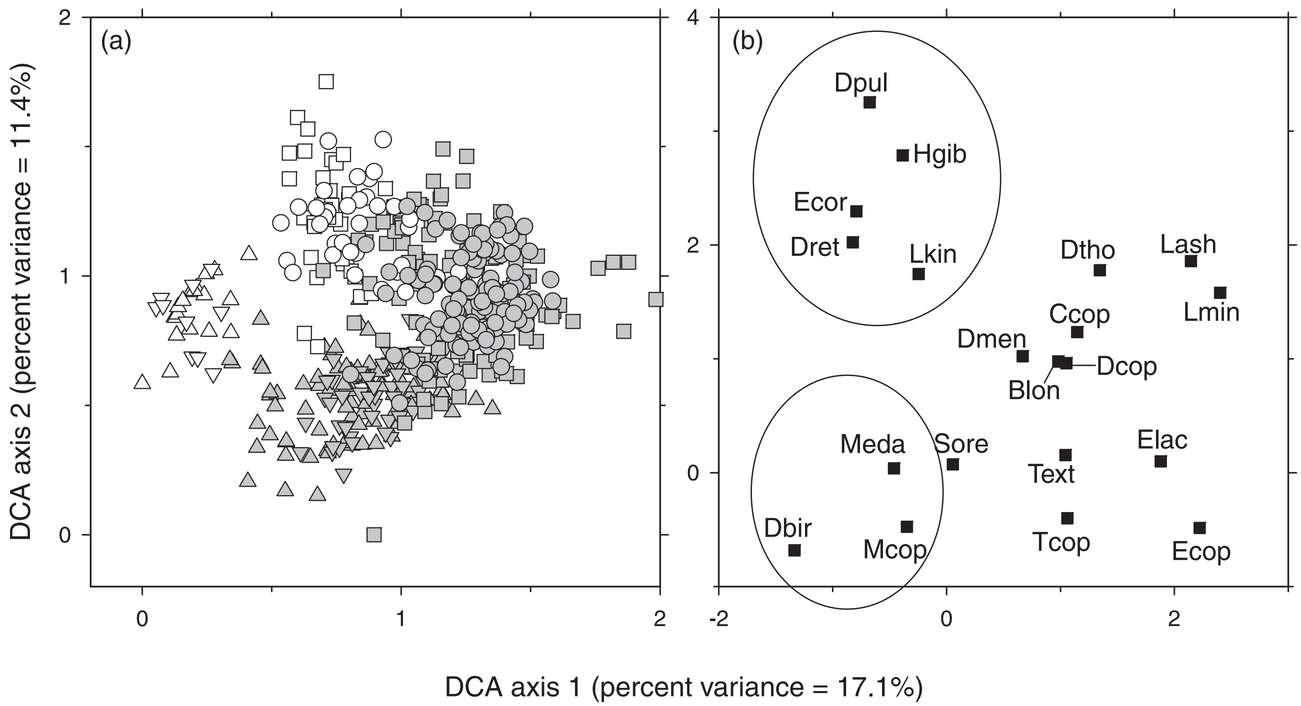
Another response seen in the initial studies on Lake Michigan and corroborated by the present study is the reduction in offshore populations of *Leptodora* (Lehman 1988, 1991). *Leptodora* populations have not been completely eliminated from the lakes, however, and substantial post-invasion populations were occasionally seen in our study. This species continues to be successful in the nearshore waters of Lake Michigan (Lehman and Cáceres 1993) and in the western basin of Lake Erie where *Bythotrephes* has never established substantial populations (Garton et al. 1990). Expansion into the open waters from these sources during periods of reduced *Bythotrephes* abundance could explain in part the occasionally large post-invasion populations that we saw. Lehman (1991) has shown a pronounced lack of spatial overlap between *Leptodora* and *Bythotrephes* in Lake Michigan, and temporal segregation has also been seen in Harp Lake (Yan and Pawson 1997), Lago Maggiore (Manca et al. 1992), and Lake Erie (Berg and Garton 1988; Johannsson et al. 1999).

The mechanism behind the negative association between these two predatory species is unclear. Initially it was thought that the decline in *L. kindti* seen in Lake Michigan was due to exploitation competition by *B. longimanus* (Branstrator and Lehman 1991; Lehman 1991; Yurista and Schulz 1995), although increases in its preferred prey *Conochilus unicornis* seen in both Lakes Huron and Michigan since its decline (M.L. Tuchman, unpublished data) argue against this. An alternate explanation is direct predation by *Bythotrephes* on *Leptodora*. There is some laboratory evidence that *B. longimanus* can capture and consume *L. kindti* (Branstrator 1995), and predation by this species has been implicated in the summer declines of *L. kindti* in Lago Maggiore (Manca and Comoli 2000).

Late summer (August and September) populations of *B. longirostris* were reported to have increased in Lake Michigan in the two years following the establishment of *Bythotrephes*, and this was attributed to the collapse of the offshore *Leptodora* population and a subsequent easing of predation pressure (Branstrator and Lehman 1991). Although post-invasion densities of *B. longirostris* in our study were not consistently higher, they showed no evidence of decline in any of the lakes, whereas the closely related *E. coregoni* exhibited sustained decreases. These results contrast with a number of studies showing that *Bosmina* is vulnerable to *Bythotrephes* predation. Allozymes of both *Bosmina* and *Eubosmina* have been found in *Bythotrephes* from Lake Michigan (Schulz and Yurista 1999), and both *B. longirostris* and *Bosmina tubicen* have declined catastrophically in Harp Lake since the *Bythotrephes* invasion (Yan and Pawson 1997; Yan et al. 2001). Mesocosm experiments have also demonstrated the susceptibility of *Bosmina* to *Bythotrephes* (Wahlström and Westman 1999), and feeding experiments on natural offshore zooplankton communities from Lake Huron have shown no substantial difference in selectivity between *E. coregoni* and *B. longirostris* (Vanderploeg et al. 1993). At present, therefore, it is hard to explain the contrasting responses of *E. coregoni* and *B. longirostris* to the arrival of *Bythotrephes*.

Holopedium gibberum, which decreased in all lakes in our study, has also been shown to be consumed by *Bythotrephes*

Fig. 12. Results of detrended correspondence analysis of (*a*) samples and (*b*) species for 1983–1999 late summer zooplankton densities in Lakes Michigan (□), Huron (○), and the central (△) and eastern (▽) basins of Lake Erie. Open symbols, pre-invasion years; solid symbols, post-invasion years. Species abbreviations are as follows: Dpul, *Daphnia pulicaria*; Hgib, *Holopedium gibberum*; Ecor, *Eubosmina coregoni*; Dret, *Daphnia retrocurva*; Lkin, *Leptodora kindti*; Dtho, *Diacyclops thomasi*; Lash, *Leptodiaptomus ashlandi*; Lmin, *Leptodiaptomus minutus*; Ccop, cyclopoid copepodites; Dmen, *Daphnia mendotae*; Blon, *Bosmina longirostris*; Dcop, diaptomid copepodites; Meda, *Mesocyclops edax*; Sore, *Skistodiaptomus oregonensis*; Text, *Tropocyclops extensus*; Elac, *Epischura lacustris*; Dbir, *Diaphanosoma birgei*; Mcop, *Mesocyclops edax*; Tcop, *Tropocyclops* copepodites; Ecop, *Epischura* copepodites. Taxa whose position in ordination space suggest a greater importance in pre-invasion communities are circled.



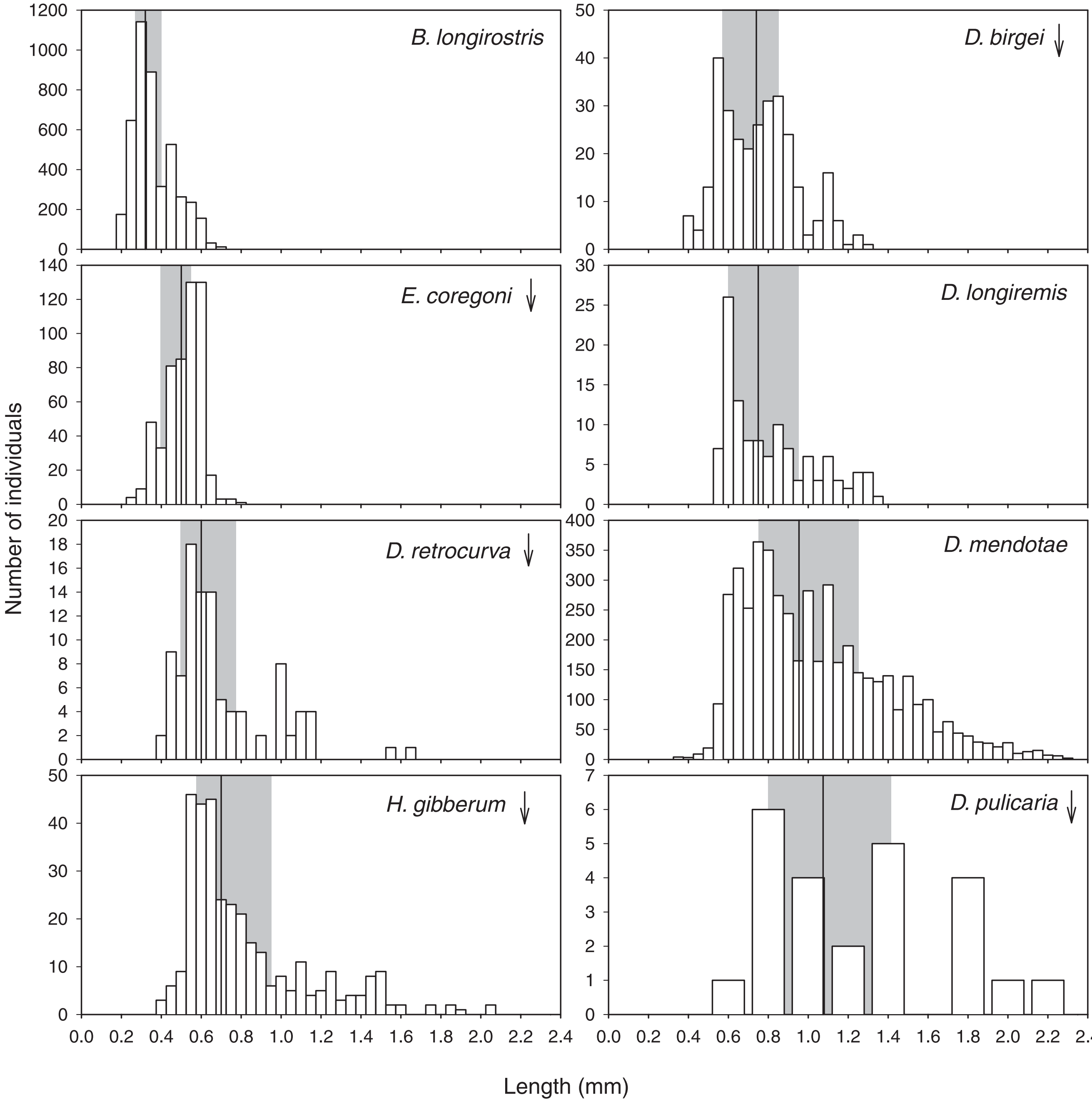
on the basis of both allozyme (Schulz and Yurista 1999) and mesocosm (Wahlström and Westman 1999) studies. In Harp Lake, however, there has been no decline in *H. gibberum* after the *Bythotrephes* invasion (Yan et al. 2001). *Diaphanosoma birgei*, which declined in our study, has also decreased in Harp Lake (Yan et al. 2001).

In our study, size, and particularly small size, did not appear to be a good predictor of population decline subsequent to *Bythotrephes* invasion. Although Yan et al. (2001) documented an overall increase in cladoceran size since the *Bythotrephes* invasion of Harp Lake, this did not appear to be the case in the Great Lakes, where the largest cladoceran, *D. pulicaria*, was apparently eliminated while the smallest, *B. longirostris*, suffered no negative effects. Makarawicz et al. (1995), examining data from Lake Michigan between 1984 and 1992, showed a marked decline in mean cladoceran length between 1986 and 1987, although this was not sustained. Species with contrasting responses to *Bythotrephes* showed a high degree of overlap in lengths, as was the case with *D. birgei* and *D. longiremis*, for example. It seems likely, therefore, that characteristics other than size play a role in determining the vulnerability to *Bythotrephes* predation. These could include morphological defenses, behaviors that reduce spatial overlap, or escape responses.

The development of diurnal vertical migration (DVM) by *D. mendotae* has been offered as a possible mechanism accounting for its reduced susceptibility to the visually feeding *Bythotrephes* (Schulz and Yurista 1999). An earlier report (Wells 1960) had indicated that the depth of migration for both *D. retrocurva* and *D. mendotae* in 1954 did not exceed 20 m, and Lehman and Cáceres (1993) reported a shift to more extreme DVM in *D. mendotae* after the introduction of *Bythotrephes*. *Daphnia mendotae* currently undergoes very pronounced DVM in Lake Michigan (Barbiero et al. 2004). Why only *D. mendotae* should have developed enhanced DVM and why this should have happened in at least three different lakes, however, remains unclear.

A consistent, but somewhat unexpected, consequence of the *Bythotrephes* invasion was the precipitous decline in densities of *M. edax* in all three lakes. *Mesocyclops edax* was also reported to have disappeared from Harp Lake after the arrival of *Bythotrephes* (Yan and Pawson 1997). *Mesocyclops edax* preys upon smaller crustaceans (Brandl and Fernando 1975; Williamson and Magnien 1982) and a variety of rotifer genera including *Asplanchna*, *Keratella*, *Polyarthra*, *Conochilus*, *Kellicottia*, and *Synchaeta* (Gilbert and Williamson 1978; Williamson and Gilbert 1980; Williamson and Magnien 1982). Feeding experiments have consistently shown that adult copepods are not preferred food items of *Bythotrephes* (Vanderploeg et al. 1993; Schulz and Yurista 1999; Wahlström and Westman 1999). This, coupled with the lack of declines seen in *B. longirostris* and total rotifer numbers (M.L. Tuchman, unpublished data) after the *Bythotrephes* invasion, makes it hard to explain the response of *M. edax*. However, ample evidence exists that nauplii are utilized by *Bythotrephes* and that these might in fact be pre-

Fig. 13. Size–frequency distributions of *Bosmina longirostris*, *Eubosmina coregoni*, *Daphnia retrocurva*, *Holopedium gibberum*, *Diaphanosoma birgei*, *Daphnia longiremis*, *Daphnia mendotae*, and *Daphnia pulicaria* for Lakes Michigan and Huron and the eastern basin of Lake Erie during late summer, 1994–1999. Vertical reference lines indicate median lengths, shaded areas indicate interquartile ranges, and arrows indicate species showing distinct declines in post-invasion years.



ferred prey of juveniles (Nauwerk 1993; Vanderploeg et al. 1993; Schulz and Yurista 1999). It is possible that *M. edax* nauplii are particularly vulnerable to *Bythotrephes* predation and that the declines in its populations are due to losses incurred during the naupliar stage. Predation by juvenile *Bythotrephes* has been estimated to constitute 44% of total lifetime consumption (Yurista and Schulz 1995), so these losses could be substantial.

It has been suggested that *Bythotrephes* predation should have less impact on the Lakes Erie and Huron zooplankton communities than on those of Lake Michigan (Yurista and Schulz 1995) because of the smaller sizes of *Bythotrephes* in Lakes Erie and Huron and the higher reported abundances in Lake Michigan. Information on lake-specific sizes of *Bythotrephes* derives largely from reports by Berg and Garton (1988) and Garton et al. (1990) for Lake Erie, Vanderploeg et al. (1993) for Lake Huron, and Yurista and Schulz (1995) for Lake Michigan. Our results show that the changes in zooplankton communities across the four regions examined after the *Bythotrephes* invasion were surprisingly uniform and that lengths of *Bythotrephes* in Lake Michigan were not greater than those in the other regions examined, with the exception of the central basin of Lake Erie, although volumetric densities were actually higher in Lake Erie than in the other two lakes considered here. Areal densities calculated from deep tows collected by our program for the two years that are currently available (1998 and 1999) generally confirm the differences in volumetric densities reported here and indicate lowest densities in Lake Michigan, highest densities in Lake Erie, and intermediate densities in Lake Huron (Barbiero et al. 2001; Barbiero and Tuchman 2002). Bilkovic and Lehman (1997) appears to be the only other report to compare sizes of *Bythotrephes* among these three lakes using data derived from a single study, and their results largely agree with our own, i.e., smaller individuals in the central basin of Lake Erie compared with Lakes Huron and Michigan. These authors noted that, in spite of differences in dry weight, lipid concentrations of *Bythotrephes* in the central basin were equal to, or higher than, those for the other lakes, suggesting that food limitation was not responsible for their smaller size. Instead, they suggested that a smaller deep-water refuge from visually feeding planktivores might explain the smaller size of *Bythotrephes* in that region of Lake Erie. Our results are not inconsistent with their hypothesis. The perception that *Bythotrephes* has had minimal impact in Lake Erie is probably due to the fact that most studies of it have been restricted to the western basin, where large populations have never become established (Berg and Garton 1988; Garton et al. 1990).

Our results indicate that *Bythotrephes* has had dramatic, sustained effects on the zooplankton communities of Lakes Michigan, Huron, and Erie. Impacts on the crustacean communities have been consistent across the lakes, in spite of differences in lake morphometry and trophic state, and have also agreed in large part with findings from the only other North American lake for which detailed information is available (Yan and Pawson 1997; Yan et al. 2001). These results indicate that invertebrate predators in general, and invasive ones in particular, can have profound effects on zooplankton community structure, even in systems that have served as models for the role of vertebrate planktivory fish on zooplankton populations (Wells 1970).

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